10.

Compensating Reactions to the Loss of the Lower Jaw in a Cave Fish.

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(Plate I; Text-figures 1-2).

Introduction.

Malformations of the head of teleosts have frequently been described and form the basis of a considerable part of the literature of fish teratology. These items chiefly concern loss or poor development of certain cranial elements, aside from the purely monstrous, such as partial twinning, either spontaneous or experimentally induced. They fall into three natural causative groups; injury and developmental (either genetically or environmentally induced). Although it is frequently impossible to be absolutely certain which a given case represents there are frequently good presumptive indications of origin. A curious case of cephalic abnormality, different from any so far described, and with certain interesting implications, appeared in connection with studies on the Mexican blind characins and forms the basis of the present communication.

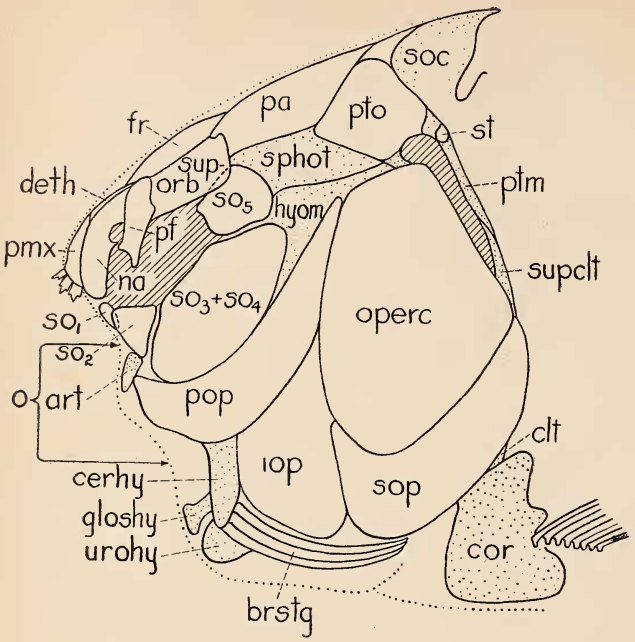
The author is grateful to Mr. Albert Greenberg of Tampa, Florida, for the privilege of studying this specimen. Mr. Greenberg, an accomplished fish culturist, who has reared thousands of this form, *Anoptichthys jordani* Hubbs and Innes, has seen only this single specimen, which was hatched in his establishment. He also kindly supplied the data on its behavior in life. Thanks are due to Mr. Paul Benzer who was kind enough to clear and stain the fish for the study of the skeletal elements. Dr. W. K. Gregory and Dr. Myron Gordon kindly contributed critical comments on the manuscript.

Description.

The general external aspect of the head of the fish here considered is shown in Plate I. The lateral view shows the front of the head to be obliquely truncate. Viewed ventrally it can be seen that the oral orifice is a slightly asymmetrical vertical slit extending from what is evidently the anterior end of the hyoid apparatus upwards to a point somewhat behind the pointed "snout." This fish fed, respired and grew to a standard length of 37 mm. in six months in spite of this malformation of the oral apparatus. Food was taken in with the accompaniment of side to side movements of the sides of the vertical "mouth," while the fish fed at an angle of about 45° to the bottom when first noted and later at an angle of nearly 90° according to Mr. Greenberg's observations. Growth was in keeping with the normal tank mates for the first three months of life but after that was slower. This slowing of growth approximately coincided with the change in feeding posture. The cause of death is unknown, but the preserved fish showed no evidence of malnutrition and it seems that direct starvation did not occur.

The basic nature of this peculiar fish head was evident only by staining and clearing and is shown in Plate I. The skull as sketched by camera-lucida is given in Text-figure 1, in which the outlines of the incompletely ossified dermal bones are indicated. The prominent difference from the normal skull is the absence of the dentary and maxillary. The angular and quadrate could not be found and evidently they too are absent. The other skull bones are all intact and most are identifiable as is indicated by the lettering. There is no evident suture between so_3 and so_4, making the elements of this series somewhat uncertain although the rest appear in their normal relative positions. The variations in the suborbitals of these cave fish, especially so_3, have been noted by Breder (1944) and this apparent fusion may have no direct connection with the other peculiarities of this particular specimen. The identification of the ceratohyal, glossohyal and urohyal is provisional. These items are of minor importance, however, to the present considerations.

The most remarkable and striking feature of this skull is the manner in which the angled preopercular bones have grown for-



TEXT-FIG. 1. Skull of cave fish with lower jaw absent. **art**—articular, **brstg** — branchiostegal, **certhy** — ceratohyal, **clt** — cleithrum, **cor**— coracoid, **deth**—dermethmoid, **fr**— frontal, **gloshy** — glossohyal, **na**— nasal, **o** — oral opening, **operc**— opercular, **pa**—parietal, **pf**—prefrontal, **pmx** — premaxilla, **pop**— preopercular, **ptm**—post-temporal, **pto**—pterotic, **so**—suborbital, **soc**— supraoccipital, **sop** — subopercular, **sphot** — sphenotic, **st** — supratemporal, **supclt** — supracleithrum, **suporb** — supraorbital, **urohy** — urohyal. See text for full explanation.

ward and inward to form the biting vertical "jaws" of this psuedo-mouth. The remaining elements of the skull have all shifted and changed their form slightly, fitting to the new conditions, as may be noted by a comparison with Plate I and Text-figure 2, B, both of which show a normal blind-fish skull. The tooth-bearing premaxilla is remote from the new oral opening as may be noted in Text-figure 1 in which arrows from "0" indicate the vertical extent and position of this orifice. Actually the central teeth form the greatest anterior reach of the fish and could in no way be supposed to be able to function in reference to food. The noncranial skeletal elements, except the associated pectoral girdle, appeared normal in every way as did the intact body of the fish posterior to the head.

The modifications of the musculature accompanying these changes could not be worked out on this single specimen, first because such myological dissection on so small a fish before the disposition of the bones was known would have been impracticable and later after clearing such dissection was impossible.

Discussion.

Since respiration and food prehension are essential activities from shortly after hatching in such fishes, it follows that in order for this jawless fish to survive, it had to "improvise" the required apparatus to an extent which was adequately functional at the proper early time. This immediate need has distinct bearing on the possible genesis of this abnormality.

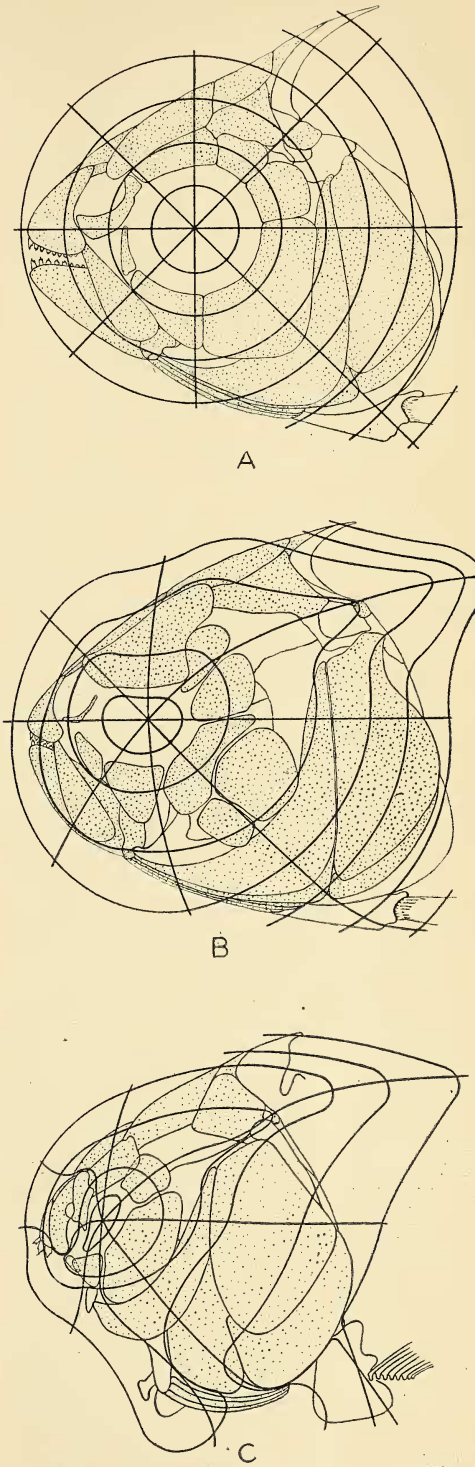
The likelihood of it being traumatic seems very remote, if not fully impossible. Such an injury to this kind of a fish larva would be certainly lethal because of the extreme delicacy and fragility during this period of life. Furthermore the symmetry of the skull would make such an accident most unlikely. A rebuilding of the face in time to have it functionally useful would be clearly impossible. Injury at a later time has these last two difficulties still present and in addition the whole head and pectoral girdle would hardly show just this kind of transformation as a consequence, after the skull had ossified normally.

Considering the two types of developmental modification possible, that of environmental effect would seem to be ruled out on the basis that this egg was one of a batch of more than one hundred hatched along with it. The rest were all normal and furthermore there is no known environmental condition that would lead to just this kind of modification and leave the rest of the fish unaffected. Considering the cause of such abnormalities as due to a retardation of development as elaborated by Stockard (1921), it is hard to imagine how any environmental accident to this single egg could lead to such a type of malformation. Consequently if actually either of the above two possible causes did not operate, the only alternative left is to suppose that the defect is genetic in origin. Due to the early need of a properly functioning mouth, as above indicated, it would seem that the basic pattern of this newly formed type of face must have been established early in the egg.

Whether or not it is a rare mutant must be left until sufficient time has elapsed to see if others appear in the same strain. This is a long inbred stock, now in its eleventh generation, and the present is the first to show this deficiency. The only other defect noted in thousands of individuals were three or four cases of slight kyphosis.

Since the specimen eventually died of some obscure cause at an age of about six months, after growing at a normal rate for the first half of its life and showed no evidences of starvation, it is difficult to associate death clearly with the malformation. Its reduction of rate of growth, however, is evidence that there was some factor involved which worked against its continued existence. Judging from the shape of the face it would seem to have no great difficulty in obtaining food from the bottom after the manner of its kind if at an angle of nearly 90° as noted by the observer. The change from an earlier feeding position of 45° may have been associated with a change in the proportions of the face with growth. It may be noteworthy in this connection that these fishes tend to become more prognathous as they develop. Since starvation seems not to be involved, it may well be that some other associated difficulty not evident from the preparations may have been the cause of death or even some cause not in the least associated with the condition.

In the native habitat of these fishes there is no food problem for the bottom is deeply floored with food substances as shown by Breder (1942). Presumably practically any form of face could obtain nourishment under such conditions, and furthermore this one did so under less advantageous circumstances as found in a hard-floored aquarium with separate food particles supplied from time to time, competing successfully with its normal tank mates. Since no such cases have come from the cave which is inhabited by this form, although in all relatively few have been collected, as compared to the thousands raised by Mr. Greenberg, inquiry may be made into the possibilities of such survival in the native state. They seem to be several in number. (1) If a rare recessive mutant, it may be that it has only been brought out by the close inbreeding and back crossing and could hardly be expected to be found or established in a larger wild population. (2) It may be that it is not a rare mutant and of more or less regular occurrence but of such a nature that its late survival is exceedingly rare. This could be because of associated but less evident deficiencies or because of a more usual failure of the remaining parts to succeed in forming a successfully functional mouth of an adequate type. (3) It may be that actu-



TEXT-FIG. 2. Transformations of polar coordinates centered in the eye. **A.** Normal-eyed river fish. **B.** Fully blind specimen from La Cueva Chica. **C.** Aquarium reared descendent from La Cueva Chica stock with lower jaw missing. Two upper figures from Breder (1944).

ally it is rare only in that successful competition with normal individuals is unusual and the present case is one of those chance survivals of an individual primarily unfit. If this latter is true it may be that the slowing of growth actually was a stunting, if not a starvation effect, because of a slightly inadequate diet due to competition in the presence of a limited food supply.

An extension of the polar coordinates used by Breder (1944) is shown in Text-figure 2. Unlike the smooth flowing regularity of the fish therein discussed, concerned with the progressive reduction of the eye, the present loss of a terminal member involves the lines of the grid in a most complicated fashion. However here again it was found that the concentric ordinates were largely of an exponential nature while the radial ones were not.

While the exact operation of these extemporized jaws is not clear, due to the impossibility of working out the myology, it would appear that since the preopercle is attached to the operculum, as the latter lifts in respiration there would be a tendency for the former to press inwards once its anterior edge was freed of its normal anchorage. Thus it is not unreasonable to suppose that the whole opercular series rocked back and forth so as to open the mouth or gill-cleft alternately, which operation would cause the opening and closing of the false jaws and provide both for respiration and feeding requirements. Evidently the swallowing and pumping mechanism was suitably functional.

Most other malformations of fish heads that have been reported from time to time are clearly of other genesis and significance. The so-called pug-headed condition in fishes which is not particularly uncommon would seem most likely to be a true achondroplasia induced by some pituitary disturbance. Gudger (1929 and 1933) discusses at length some such cases and gives a history of the literature of that subject. Whatever the cause of the present condition, it would seem not likely to be associated with an endocrine difficulty, since there is no known disfunction of this sort leading to anything even remotely resembling the present condition.

Another cephalic abnormality, of less frequency, is the so-called "two-mouthed" condition which is reviewed by Gudger (1930). This is evidently a purely traumatic condition in which the floor of the mouth has been torn open so that the hyoid apparatus is detached from the lower jaw just behind the symphasis. This clearly has no relation to the present problems nor has the side to side mouths of imperfectly separated twin heads.

The reports of fully or partially occluded mouths, which may or may not be accompanied by the loss of associated skeletal elements, would seem to be most nearly related to the present condition, but no specimens previously reported have been able to improvise functional "jaws" out of the remaining parts. Nor have the preopercular bones, in these cases, shown any detachment of their anterior ends, a prerequisite to the functioning of such false "jaws." In these other cases dermal tissues have overgrown the places that would have normally been occupied by the missing bones, reducing the mouth to a more or less ineffectual orifice. While achondroplasia may enter into these cases, they are frequently far from the typical pug-headed condition. It is perhaps pertinent that all such cases of occluded mouths with loss of bony elements refer to the Ostarophysi, specifically to the Cyprinidae and the Catosomidae, and most of these to *Cyprinus carpio* Linnaeus. See for example Lawrence (1875), Fehlmann (1912) and Spillmann (1938). On the other hand the true pug-headed condition is widespread in many groups of fishes. Dean (1916) under "teratology" gives a long list of references to both types of malformation.

The series of studies on this form of blind fish has shown evolutionary changes almost entirely in the nature of loss. The only exception so far found has been that involving an increase in the chemical sense organs. The taste buds have shown a numerical increase and the nasal capsule some modification as has been indicated by Breder and Rasquin (1943). Those features involving the supporting architectural elements are all of loss as well as those of eye and ear, Breder (1943). Whether there is an associated tendency to drop other structures related to a dark, protected environment with an abundance of food present, somewhat after the fashion of an intestinal parasite, poses a rather pretty problem on which the following has a distinct bearing. Do these fish regularly show an early mortality due to the production of an unusually large number of defective individuals doomed to disappear shortly after hatching? The preservation of large numbers of newly hatched young could determine this with some degree of accuracy. If such losses in general are of the magnitude of the present example it should not be surprising that few develop to a macroscopic size.

Summary.

1. A single specimen of blind characin, one of a normal brood, developed with the lower jaw completely absent and lived to reach a standard length of 37 mm.
2. The front end of each preopercular bone grew forward and around in front of the face to form a "mouth" which formed

a vertical slit, the "jaws" working from side to side by means of which the fish both fed and respired.

3. Growth was normal for the first three months of life but later became retarded.
4. This is evidently a genetic loss and in order for the improvised buccal apparatus to be adequately functional soon enough, the development must have formed early, very likely its main features being established within the egg.
5. This specimen is unique among the reported cases of cephalic abnormalities in fishes, in that it developed a substitute jaw mechanism.

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EXPLANATION OF THE PLATE.

PLATE I.

Fig. 1 Lateral view of cave fish lacking lower jaw.

Fig. 2. Ventral view of same specimen.

Fig. 3. Lateral view of cleared head of cave fish lacking lower jaw.

Fig. 4. Lateral view of cleared head of a normal cave fish.

(A.M.N.H. photographs).

FIG. 1.

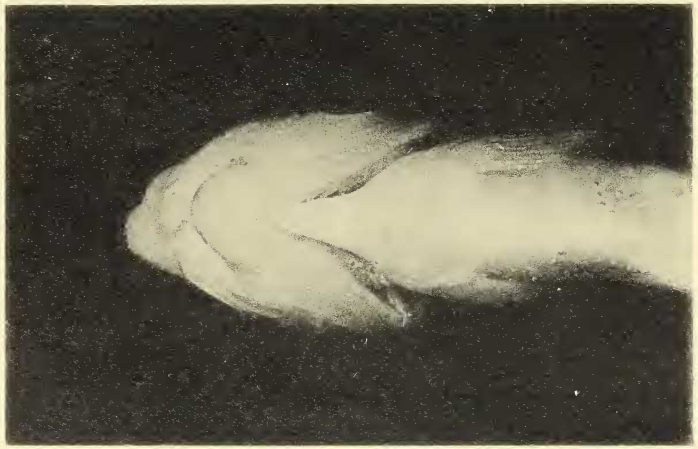

FIG. 2.

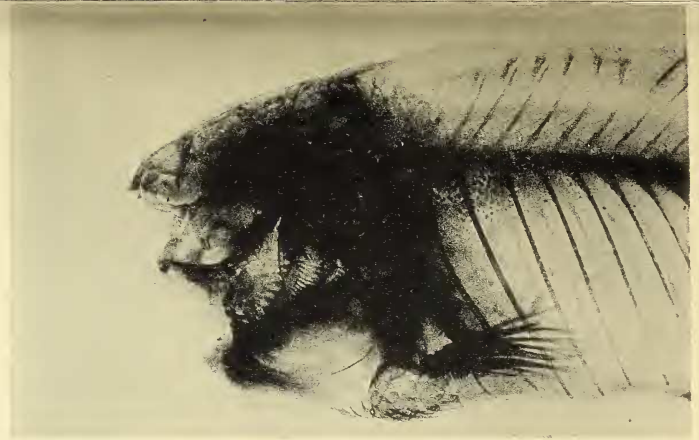

FIG. 3.

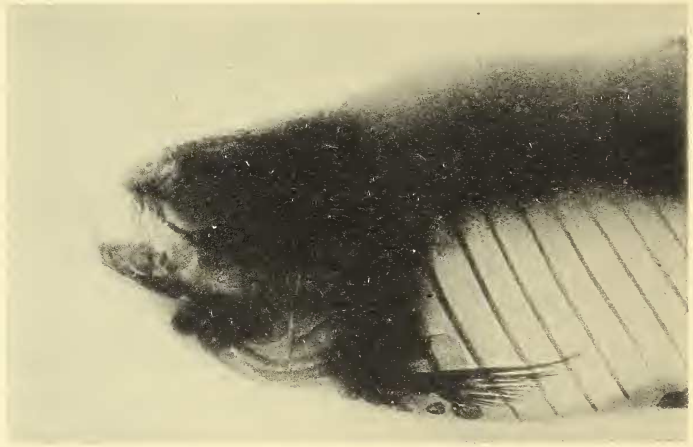

FIG. 4.

COMPENSATING REACTIONS TO THE LOSS OF THE LOWER JAW IN A CAVE FISH.